

# Integrating arthropod herbivory and reduced herbicide use for weed management

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Few studies have examined the combined effect of herbicide-induced stress and arthropod herbivory to reduce weed fitness. The purpose of this study was to quantify the effect of arthropod herbivory on the herbicide dose–response of a perennial weed. Fluroxypyr dose–response bioassays using volunteer potato were conducted in the presence and absence of Colorado potato beetle (CPB) herbivory. Logistic model parameter estimates for leaf area, shoot biomass, tuber number, and tuber biomass were often lower with herbivory, compared with no herbivory. Greater variance of parameter estimates within herbivory plots was attributed largely to differential feeding because CPB density was not manipulated in the field. Results from short-season field studies (1,000 growing degree days [GDD] after postemergence [POST] herbicide application) indicated that herbivory had the most effect on potato during a period that coincided with high CPB density and optimal temperatures for CPB development. Season-long bioassays (> 3,100 GDD after POST) revealed that addition of herbivory reduced herbicide use 65 to > 85%, compared with the dose needed to achieve the same reduction in tuber production in the absence of herbivory. Integrated weed management systems targeting volunteer potato are more effective when fluroxypyr applications are made before periods of high herbivory. Moreover, this article describes an experimental approach contributing to optimization of combined effects of arthropod herbivory and reduced herbicide doses.

**Nomenclature:** Fluroxypyr; volunteer potato, *Solanum tuberosum* L.

**Key words:** Biological weed control, biologically effective dose, dose–response, integrated weed management, logistic model, reduced herbicide dose.

Integrated weed management (IWM) seeks to manage weed populations through a series of mortality and fitness-reducing events. Arthropod herbivory, as one aspect of biological control, is a component of IWM. Biological control has been most common in range, pasture, and aquatic environments, where a nonindigenous agent is imported to manage an exotic pest (Andres 1982; Charudattan 1986; Sheley and Rinella 2001). Incorporating biological control into an IWM system for annual row crop production has been limited.

Past studies of interactions between herbicide use and arthropod herbivory have typically focused on the effect of herbicide toxicity or host plant quality on arthropod fitness and rarely on how a combination of herbicide use and arthropod herbivory affects weed fitness (Ainsworth 2003; Campbell 1988). Although the root-feeding weevil, *Cyphocleonus achates* Fahraeus, had no detectable impact on spotted knapweed (*Centaurea maculosa* Lamarck), reduced rates of picloram did not limit weevil establishment (Jacobs et al. 2000). Kjær and Elmgaard (1996) found that chlorsulfuron applications to wild buckwheat (*Polygonum convolvulus* L.) decreased fitness of the leaf-eating beetle, *Gastrophysa polygoni* L., despite no direct toxicity of the herbicide to the beetle. Wild buckwheat biomass was greatly reduced by chlorsulfuron (Kjær 1994), but the contribution of the beetle, *G. polygoni*, to weed suppression was not evaluated.

Speight and Whittaker (1987) quantified the effects of the chrysomelid beetle *Gastrophysa viridula* and the herbicide asulam on broadleaf dock (*Rumex obtusifolius* L.) fitness. Their results suggest that the effect of herbicide-in-

duced stress and beetle herbivory on weed suppression may be dependent on herbicide dose. The combination of *Aphthona* spp. flea beetles and picloram plus 2,4-D increased leafy spurge (*Euphorbia esula* L.) control when compared with either method used alone (Lym and Nelson 2002; Nelson and Lym 2003). Combining feeding by the gall-forming mite, *Aceria malherbae* Nuzzaci, with 2,4-DB or glyphosate application was more effective at reducing field bindweed (*Convolvulus arvensis* L.) growth than either tactic alone (Boydston and Williams 2004). There are few studies that permit determination of the importance, at an IWM level, of interactions between arthropod herbivory and herbicide use (Norris and Kogan 2000).

In climates where potato tubers persist over winter, volunteer potato is commonly a weed in rotational crops of potato (Lutman 1977a; Williams and Boydston 2002). It is very competitive in crops that are slow to emerge and causes substantial yield losses. Volunteer potato shoots tend to senesce after crop canopy closure, although weed growth continues in crops that produce little shade, e.g., onions (*Allium cepa* L.) and carrots (*Daucus carota* L.). Like several solanaceous weeds, volunteer potatoes are a host to serious diseases, insects, and nematodes of potato (Ellis 1992; Thomas 1983). Volunteer potatoes are difficult to suppress because of large food reserves in the tuber and the ability to resprout (Williams and Boydston 2002). Depending on the crop, primary management tactics include altering the planting date, soil fumigation, tillage, hand-weeding, or herbicide application (or all). Recommended doses of herbicides such as bromoxynil, fluroxypyr, and glyphosate often do not control

TABLE 1. Dates of planting, herbicide application, and harvest for short-season (1,000 GDD after herbicide application) and season-long (> 3,100 GDD after herbicide application) field bioassays at Roza and Paterson, WA.<sup>a</sup>

Experiment	Year	Location	Period	Planting date	Herbicide application date	Harvest date
Short-season	2002	Roza	Early	April 22	June 10	July 15
			Late	June 14	July 10	August 7
	2003	Roza	Early	April 21	May 30	July 7
			Late	June 11	July 9	August 6
		Paterson	Early	April 9	May 20	June 24
			Late	June 12	July 9	August 4
Season-long	2003	Roza	—	April 21	May 30	September 11
		Paterson	—	April 9	May 20	September 2

<sup>a</sup> Abbreviation: GDD, growing degree days.

volunteer potatoes, and tubers continue to be produced, even when combined with other management tactics (Boydston 2001; Boydston and Seymour 2002).

The oligophagous Colorado potato beetle (*Leptinotarsa decemlineata* Say.) (CPB) is native to southwestern North America. The CPB feeds primarily on solanaceous species, and native hosts were buffalobur (*Solanum rostratum* Dunal), silverleaf nightshade (*Solanum elaeagnifolium* Cavanilles), and *Solanum angustifolium* Miller. (Hsiao and Fraenkel 1968). Studies have found that CPB has two generations per year in the Pacific Northwest, with larval and adult feeding overlapping with volunteer potato growth (Xu and Long 1997). Extensive defoliation from CPB during blooming can reduce potato yields (Hare 1980; Zehnder and Evanylo 1989) and potato competitiveness (Jansson and Smilowitz 1986). The occurrence of CPB in potato rotation crops has not been reported, although preliminary surveys have observed volunteer potato-infested fields without CPB (M. Williams and D. Walsh, unpublished data). Absence of CPB in rotation crops may be explained by larval and adult mortality as the result of insecticide applications targeting arthropod pests. The extent to which herbivory may be an additional tool for managing volunteer potato is unknown.

The goal of this study was to evaluate a model study system that coupled herbicide use with arthropod herbivory for management of a persistent weed of crops grown in rotation with potato. The objective was to quantify the influence of CPB herbivory on the response of volunteer potato to herbicide dose. Fluroxypyr was chosen because the herbicide is used in several potato rotation crops of the Pacific Northwest, does not control potatoes at the recommended dose of 280 g fluroxypyr ae ha<sup>-1</sup>, and CPB has been observed on treated plants.

## Materials and Methods

### Larval Feeding

Tests were conducted in the greenhouse to assess the effect of CPB larval feeding on the fluroxypyr dose-response of potato. Potatoes cv 'Russet Burbank' were grown from 55-g tubers and thinned to a single stem after emergence. When the study was repeated, developed eyes were cut from whole tubers to minimize the number of stems per plant. Tuber pieces were coated with thiophanate-methyl and mancozeb.<sup>1</sup> A sand-peat mixture was used to fill 7.6-L pots, and the single tuber or tuber piece was placed 5 cm below the surface.

The experimental design was a randomized complete block with six replications in a 6 by 2 factorial arrangement of herbicide "dose" and CPB "herbivory." Doses of 0, 2.2, 8.8, 35, 140, and 560 g fluroxypyr ae ha<sup>-1</sup> were selected to obtain a range of physiological and morphological responses. When potatoes had five leaves and were approximately 20 cm tall, fluroxypyr was applied in a vented spray chamber with an even flat-fan nozzle delivering 280 L ha<sup>-1</sup> at a pressure of 180 kPa. Egg masses of CPB were collected from a local potato field and incubated at room temperature until hatch. The herbivory factor had two levels: presence or absence of CPB larvae. Within 2 d after herbicide application, the herbivory treatment was imposed by placement of 25 first instars on appropriate plants. Pots were arranged on the bench to avoid plant-to-plant contact so that larvae could not move off assigned potatoes. After 2 d, CPB were thinned to 20 larvae per plant. Experiments were terminated when no leaf tissue was available for larval feeding in the highest dose treatment. Beetles were removed by hand, and stems were clipped at the soil surface. Leaves were separated from stems, and leaf area was determined using a leaf area meter.<sup>2</sup> All leaves and stems were oven-dried to constant weight, and final shoot biomass was recorded. Greenhouse temperature was maintained at 28 ± 5 C throughout the duration of each experiment.

### Field Bioassays: Short-season

Field tests were used to assess the effect of short-term CPB feeding on the fluroxypyr dose-response of potato at two times within a year. To simulate a period between volunteer potato emergence and senescence after crop canopy closure (Xu and Long 1997), treatments were initiated such that potato fitness was assessed 1,000 ± 35 growing degree days (GDD) (base 4.4 C) after herbicide treatment. The study was repeated so that (1) potato emergence approximately coincided with natural emergence of the first and second generation of CPB adults and (2) potato growth occurred after both a typical early and late planting date of a rotation crop, such as sweet corn (*Zea mays* L.). This replication in time, within a season, is referred to hereafter as "early" and "late" period (Table 1).

Field experiments were conducted at Prosser, WA, in 2002 and 2003, and an additional site was added at Paterson, WA, in 2003. The soil at Prosser was a Warden sandy loam (coarse-silty, mixed, superactive, mesic Xeric Haplocambids), with 1.1% organic matter and pH 7.2. The soil

at Paterson was a Quincy sand (mixed, mesic Xeric Torrip-sammments), with 0.5% organic matter and pH 7.0. During April and June (Table 1), whole potato tubers (85 g), cv Russet Burbank, were planted 12 cm deep and spaced 86 cm apart. Plots were fertilized and irrigated according to soil tests and Washington State University recommendations. Pendimethalin, a standard herbicide used for weed control in potatoes, was applied at a dose of 1.1 kg ha<sup>-1</sup> preemergence. Emerging weeds were removed by hand.

Experiments used a randomized complete block design with seven replications. A single plant served as an experimental unit. The treatment design was a 4 by 2 factorial arrangement of herbicide dose and CPB herbivory, respectively. Herbicide doses used were 0, 140, 280, and 560 g fluroxypyr ae ha<sup>-1</sup>. The herbivory factor had two levels, presence or absence of feeding by naturally occurring CPB populations. When potatoes were 15 cm tall and had six leaves, fluroxypyr was applied using a compressed-air backpack sprayer delivering 190 L ha<sup>-1</sup> at 190 kPa. The absence of CPB defoliation was established by treating plants with 34 ml of a 0.6% solution of imidacloprid<sup>3</sup> within 2 wk of emergence. The insecticide was poured in a 15-cm-deep hole adjacent to the plant, which was immediately filled with soil. Plots were re-treated if larvae were observed.

CPB densities were assessed at 0, 2, or 4 wk after treatment (WAT) (or all). At each sampling time, three classes of CPB were counted on every plant, including (1) total number of first, second, and third instars, (2) total number of fourth instars, and (3) total number of adults. At harvest, leaf area and oven-dry shoot biomass were determined using the same approach as described in larval feeding studies. Potato tubers were dug by hand, and total tuber number and fresh tuber biomass were recorded.

## Field Bioassays: Season-long

In 2003, at Paterson and Prosser, field bioassays were expanded to evaluate the effect of CPB feeding on potato response to fluroxypyr dose under season-long growing conditions. Tests were established in the same way as described previously; however, the experiments spanned over both early and late periods of the short-season bioassays (> 3,100 GDD, base 4.4 C, after herbicide application) (Table 1). Experimental approach, study implementation, and plot maintenance were identical to those used in the short-season bioassays. Potato tubers were dug by hand, and total tuber number and fresh tuber biomass were recorded. Densities of CPB larvae and adults were assessed as described earlier, although potatoes were also surveyed for CPB at 8 and 12 WAT.

## Statistical Analyses

All potato data were subjected to analysis of variance. The mixed models procedure (SAS 2000) was used to determine which random effects (year, location, and period) could be combined. Based on  $P = 0.05$ , data were pooled accordingly for analysis described below.

A logistic model was used to quantify weed response over a range of herbicide doses (Seefeldt et al. 1995). Potato vegetative and reproductive data were fitted to the logistic model:

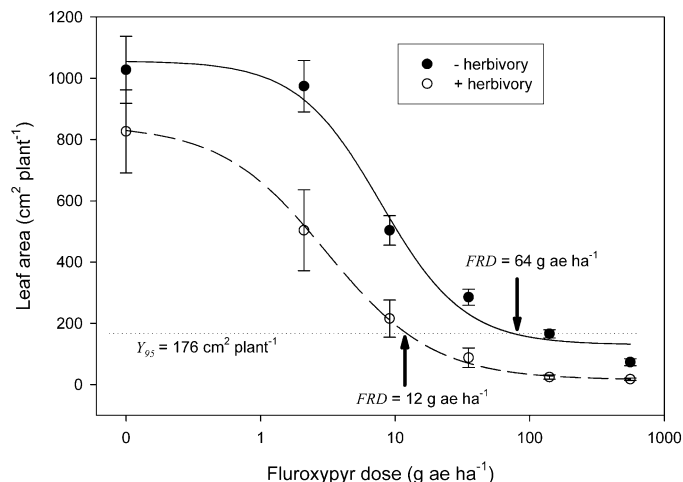


FIGURE 1. Illustration of herbicide dose-response functions with and without herbivory,  $Y_{95}$  parameter, and fixed response doses (FRD). The  $Y_{95}$  quantifies plant response that results in a 95% reduction in the absence of herbivory, relative to herbicide dose = 0. The FRD quantifies the herbicide dose required to reduce the response variable to  $Y_{95}$ .

$$y = C + \frac{D - C}{1 + (x/I_{50})^b} \quad [1]$$

where,  $y$  = response variable (e.g., leaf area),  $x$  = fluroxypyr dose,  $C$  = response at high doses (lower asymptote),  $D$  = response when dose = 0 (upper asymptote),  $I_{50}$  = dose eliciting 50% reduction in response variable, and  $b$  = the slope at the  $I_{50}$  dose. Nonlinear regression methods were used to fit potato response to fluroxypyr dose for both levels of herbivory.

Once model parameters were determined, an additional parameter was calculated. This parameter was aimed at quantifying the herbicide dose, under herbivory, required to reduce the response variable to a value equivalent to a 95% reduction in the response variable without herbivory. One approach could be to calculate an  $I_{95}$  dose specific to each dose-response function (Streibig et al. 1995). However,  $I_{95}$  doses from two separate data sets will not necessarily reflect the same plant response when other model parameters differ between data sets. Another approach, using a fixed response dose (FRD), serves as a comparison between two dose-response functions (e.g., with and without herbivory) at a fixed plant response. Figure 1 provides an illustration, where leaf area has been regressed against fluroxypyr dose. To do this, model parameters from Equation 1, in the absence of herbivory, were used to calculate a 95% reduction ( $Y_{95}$ ) in each response variable, relative to herbicide dose = 0. The equation used to solve for  $Y_{95}$  was

$$Y_{95} = (D - C) \times 0.05 + C \quad [2]$$

where  $D$  and  $C$  are the same parameters as in Equation 1. The FRD was determined by rewriting Equation 1, using the  $Y_{95}$  parameter from Equation 2, and solving for dose:

$$\text{FRD} = I_{50} \times \sqrt[b]{\frac{D - C}{Y_{95} - C}} - 1 \quad [3]$$

with parameters described above. For each response variable, an FRD was calculated for both levels of herbivory, using parameter estimates from Equations 1 and 2. FRD differed

TABLE 2. Larval feeding studies: parameter estimates for the effects of fluroxypyr dose and CPB herbivory on potato leaf area and shoot biomass (SE in parentheses).<sup>a</sup>

Response variable	Herbivory <sup>b</sup>	<i>D</i> <sup>c</sup>	<i>C</i>	<i>I</i> <sub>50</sub>	<i>b</i>	<i>R</i> <sup>2</sup>	<i>Y</i> <sub>95</sub>	FRD <sup>d</sup>
		cm <sup>2</sup> plant <sup>-1</sup>	cm <sup>2</sup> plant <sup>-1</sup>	g ae ha <sup>-1</sup>			cm <sup>2</sup> plant <sup>-1</sup>	g ae ha <sup>-1</sup>
Leaf area	–	1,057 (61)	130 (47)	8 (2)	1.4 (0.4)	0.76	176	64*
	+	848 (103)	16 (66)	3 (1)	1.1 (0.5)	0.54	176	12*
		g plant <sup>-1</sup>	g plant <sup>-1</sup>	g ae ha <sup>-1</sup>			g plant <sup>-1</sup>	g ae ha <sup>-1</sup>
Shoot biomass	–	7.2 (0.6)	2.2 (0.4)	9 (2)	1.9 (1.2)	0.54	2.5	41
	+	6.8 (0.8)	1.5 (0.6)	4 (2)	1.0 (0.6)	0.41	2.5	18

<sup>a</sup> Abbreviations: CPB, Colorado potato beetle; FRD, fixed response dose.

<sup>b</sup> Herbivory level in the absence (–) and presence (+) of CPB.

<sup>c</sup> *D* is upper asymptote; *C* is lower asymptote; *I*<sub>50</sub> is fluroxypyr dose eliciting 50% response relative to dose = 0; *b* is slope at *I*<sub>50</sub> dose; *Y*<sub>95</sub> quantifies the plant response that results in a 95% reduction in the absence of herbivory; FRD quantifies the herbicide dose required to reduce the response variable to *Y*<sub>95</sub>.

<sup>d</sup> FRD estimates followed by an asterisk differ significantly between herbivory levels based on nonoverlapping 95% confidence intervals.

significantly between herbivory levels when 95% confidence intervals failed to overlap.

## Results and Discussion

### Larval Feeding

By 8 to 11 d after application, fluroxypyr reduced potato leaf area and shoot biomass. Based on logistic model parameter estimates (*D* and *C*), fluroxypyr alone reduced leaf area and shoot biomass by up to 88 and 69%, respectively (Table 2). In the absence of herbivory, the *I*<sub>50</sub> dose for leaf area and shoot biomass was 8 and 9 g ae ha<sup>-1</sup>, respectively. Fluroxypyr has been evaluated for volunteer potato control under field conditions, providing 33 to 99% control with application rates of 220 to 600 g ae ha<sup>-1</sup> (Boydston 2001; Boydston and Seymour 2002). Response of potato to low fluroxypyr doses in this study is attributed to potatoes propagated from small tuber pieces and grown in a greenhouse environment.

Herbicide dose–response was influenced by herbivory. Leaf area was reduced by CPB feeding over all fluroxypyr doses, thus less fluroxypyr was required to achieve similar levels of leaf area reduction in the treatment with herbivory. In the absence of herbicide application (*D*), leaf area with herbivory was 20% lower compared with potato without herbivory (Table 2). The *I*<sub>50</sub> dose for leaf area was 8 g ae ha<sup>-1</sup> without feeding and 3 g ae ha<sup>-1</sup> with feeding. Similar reductions in plant size with herbivory were observed for shoot biomass. Boydston (2001) and Boydston and Seymour (2002) observed substantial midseason defoliation by CPB on volunteer potatoes that escaped herbicide and cultivation treatments.

Fitting these data to a logistic model and calculation of the *Y*<sub>95</sub> and FRD provides an approach to quantify the least amount of herbicide required to result in a practical outcome for different levels of herbivory. As an example, the *Y*<sub>95</sub> for leaf area was 176 cm<sup>2</sup> plant<sup>-1</sup>. To obtain a 95% reduction in leaf area, 64 g ha<sup>-1</sup> was required in the absence of herbivory, whereas 12 g ha<sup>-1</sup> was sufficient in the presence of herbivory (Table 2). Larval feeding studies indicate that reduced herbicide doses may be more effective when followed by arthropod herbivory.

### Field Bioassays: Short-season

Unlike greenhouse bioassays, CPB densities were less regulated in the field. Plants in the “herbivory-absent” treatment, in actuality, experienced feeding before CPB consumed a lethal insecticide dose. Live adults also were observed on imidacloprid-treated plants (Table 3); however, adults were often not feeding but mating or ovipositing. There were a few occasions where larvae were observed on imidacloprid-treated plants, which resulted in re-treatment with insecticide. Our discussion assumes that insecticide applications and the minimal defoliation those plants experienced had a negligible effect on volunteer potato leaf area, shoot biomass, tuber number, and tuber biomass.

CPB density in the “herbivory-present” treatment was not controlled. High standard errors of mean CPB density, particularly at 2 and 4 WAT, reflect a range of CPB number per plant (Table 3). Although the purpose of field bioassays was to test the study system under natural herbivore conditions in the field, a shortcoming was that plants assigned the herbivory-present treatment may not have experienced identical levels of herbivory. This is supported by parameter estimates for the *I*<sub>50</sub> dose. Standard errors of the *I*<sub>50</sub> dose for the herbivory-present treatment were typically higher than those for the herbivory-absent treatment (Table 4). Conceivably, differential feeding due to CPB density resulted in more variable potato response, compared with uniform feeding. Addressing this issue in future research will come at significantly greater expense but may be possible with larger plots, more replicates, or creating more consistent arthropod herbivory (i.e., uniform density of larval and adult stages) through the use of caging, monitoring, and regular CPB introduction and removal as needed.

CPB larvae were observed throughout the duration of the experiments. Mean population densities were generally highest 2 and 4 WAT during the late period, during the second CPB generation (Table 3). Xu and Long (1997) found that volunteer potato is an early food source for CPB in eastern Washington and that the population density of second-generation CPB is typically higher than population density of the first generation. Mean density of fourth instars ranged from 0.9 to 5.8 larvae plant<sup>-1</sup> in herbivory plots at 2 and 4 WAT (Table 3). Fourth instars consume approximately 75% of the leaf area of all larval stages combined, and one

TABLE 3. Mean larval and adult density of CPB sampled at 0, 2, and 4 WAT in short-season field bioassays (1,000 GDD after herbicide application) (SE in parentheses).<sup>a,b</sup>

Year	Location	Period	Herbivory <sup>c</sup>	0 WAT			2 WAT			4 WAT		
				LV1	LV2	AD	LV1	LV2	AD	LV1	LV2	AD
				no. plant <sup>-1</sup>								
2002	Roza	Early	— <sup>d</sup>	—	—	—	—	—	0.2 (0.5)	0.3 (0.6)	1.0 (1.1)	
		+	—	—	—	—	—	3.0 (5.5)	3.5 (6.3)	2.1 (3.1)		
2003	Roza	Late	—	—	—	—	0.8 (1.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.2)	1.0 (1.3)	
		+	—	—	—	10.8 (26.7)	0.9 (1.2)	14.5 (31.5)	4.3 (7.3)	2.1 (2.7)		
		Early	—	—	—	0.0 (0.0)	0.1 (0.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.5 (2.2)	
		+	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.6 (3.3)	1.4 (1.7)	1.0 (4.7)	0.1 (0.4)	4.2 (8.4)		
2003	Paterson	Late	—	—	—	—	6.3 (19.0)	0.1 (0.4)	1.7 (2.8)	1.3 (3.3)	1.7 (2.0)	
		+	0.0 (0.0)	0.0 (0.0)	5.3 (3.0)	1.4 (2.2)	2.5 (3.4)	2.7 (6.7)	2.7 (5.8)	0.9 (2.5)		
		Early	—	—	—	43.8 (57.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.8)	0.2 (0.8)	
		+	0.2 (0.6)	0.1 (0.3)	5.2 (2.9)	0.0 (0.0)	0.9 (1.0)	4.7 (10.4)	1.8 (3.7)	1.7 (3.4)		
2003	Paterson	Late	—	—	—	—	0.0 (0.0)	0.1 (0.3)	0.1 (0.4)	0.0 (0.0)	1.2 (2.0)	
		+	0.2 (1.1)	0.1 (0.4)	1.1 (1.3)	6.1 (8.5)	2.9 (4.7)	1.3 (5.5)	1.6 (6.0)	2.6 (5.6)		

<sup>a</sup> Abbreviations: CPB, Colorado potato beetle; GDD, growing degree days; WAT, weeks after treatment.<sup>b</sup> LV1 is total number of first, second, and third instars; LV2 is total number of fourth instars; AD is total number of adults.<sup>c</sup> Herbivory level in the absence (—) and presence (+) of CPB.<sup>d</sup> No CPB data were collected.

adult can consume as much as 9.7 cm<sup>2</sup> of potato foliage per day (Ferro et al. 1985). Mean larval and adult CPB densities were generally at or below densities observed in naturally occurring populations elsewhere (Xu and Long 1997).

The fluroxypyr dose required to reduce leaf area a set amount was less when herbivory occurred. The lower asymptote (*C*) was 0 regardless of herbivory level, indicating plants could be entirely defoliated with fluroxypyr. But period also influenced the extent of leaf area reduction (*P* = 0.02). For example, herbivory reduced the FRD for leaf area > 83% during the late period but not earlier. Also, the *I*<sub>50</sub> dose appeared to be reduced more during the late period compared with the early period, although high variance associated with the parameter estimate was noted (Table 4). Greater percent reduction in leaf area response to herbivory during the late period was, in part, the result of higher CPB densities during that time. Temperature was also a contributing factor. Air temperature during the late period was warmer than that during the early period (data not shown) and reflected optimal temperatures for CPB development and maximum daily leaf consumption (Ferro et al. 1985).

The shoot biomass response to fluroxypyr dose was influenced by location (*P* = 0.04). In the absence of both fluroxypyr and herbivory, shoot biomass averaged 250 g plant<sup>-1</sup> at Roza and 210 g plant<sup>-1</sup> at Paterson (Table 4). For Roza the *D* parameter was reduced 33% with herbivory (Table 4). High standard errors for *I*<sub>50</sub> dose make it difficult to confirm whether there were true differences in shoot biomass between herbivory levels as fluroxypyr dose increased.

Tuber number was affected by location (*P* = 0.02), with Paterson having approximately twice as many tubers as Roza (Table 4). However, at both locations, tuber number response to fluroxypyr dose was relatively unaffected by herbivory. Presence of CPB did not significantly reduce tuber number at low (*D*) or high (*C*) fluroxypyr doses (Table 4). With herbivory the *I*<sub>50</sub> dose was 42% of the treatment without herbivory at Paterson, but again, potato response in the presence of herbivory was higher than in its absence. Williams and Boydston (2002) found that potato tuber number was unaffected when shoots of six-leaf plants were removed 4 cm below the soil surface. Potato density was only reduced with two or more shoot-removal events or single shoot-removal event at the 10-leaf stage (Williams and Boydston 2002). Although CPB was observed to entirely defoliate potatoes in some plots in this study, those plants were abandoned by CPB before potato stems were consumed or regrowth occurred.

CPB herbivory had little effect on tuber biomass response to herbicide dose early but did reduce tuber biomass late (*P* < 0.01). As an example, the *D* parameter for the early period was not reduced, whereas for the late period, *D* was reduced 54% with herbivory, compared with no herbivory (Table 4). The *I*<sub>50</sub> dose was numerically reduced 47% with herbivory during the late period. Greater percent reduction in tuber biomass to herbivory during the late period, compared with the early period, was the result of higher CPB densities and optimal temperatures for maximum defoliation. Temperature- and density-dependent defoliation rates are important in establishing economic thresholds and predicting yield loss in potatoes (Ferro et al. 1985; Shields and Wyman 1984).

TABLE 4. Short-season field bioassays (1,000 GDD after herbicide application): parameter estimates for the effects of fluroxypyr dose and CPB herbivory on potato leaf area, shoot biomass, and tuber number and biomass (SE in parentheses).<sup>a</sup>

Response variable	Location	Period	Herbivory <sup>b</sup>	$D^c$	$C$	$I_{50}$	$b$	$R^2$	$Y_{95}$	FRD <sup>d</sup>
Leaf area		Early	–	cm <sup>2</sup> plant <sup>–1</sup>	cm <sup>2</sup> plant <sup>–1</sup>	g ae ha <sup>–1</sup>			cm <sup>2</sup> plant <sup>–1</sup>	g ae ha <sup>–1</sup>
			+	2.4 (0.2)	0.0 (1.0)	55 (68)	1.1 (2.9)	0.65	0.12	> 560
		Late	–	1.7 (0.1)	0.0 (0.5)	50 (83)	1.2 (3.1)	0.68	0.12	428
			+	1.2 (0.1)	0.0 (0.6)	170 (128)	1.5 (2.1)	0.48	0.12	> 560*
Shoot biomass	Roza		–	g plant <sup>–1</sup>	g plant <sup>–1</sup>	g ae ha <sup>–1</sup>			g plant <sup>–1</sup>	g ae ha <sup>–1</sup>
			+	250 (12)	47 (46)	153 (47)	1.7 (1.2)	0.58	57	> 560
		Paterson	–	164 (10)	55 (14)	96 (88)	3.2 (8.5)	0.42	57	401
			+	210 (22)	11 (45)	77 (101)	2.0 (5.5)	0.51	57	141
	Paterson		–	212 (25)	9 (41)	50 (449)	2.4 (2.3)	0.47	57	81
			+	no. plant <sup>–1</sup>	no. plant <sup>–1</sup>	g ae ha <sup>–1</sup>			no. plant <sup>–1</sup>	g ae ha <sup>–1</sup>
		Roza	–	8.9 (0.8)	1.6 (1.3)	277 (72)	10.2 (230)	0.34	3.7	302
			+	9.3 (0.6)	0.0 (2.3)	251 (76)	2.3 (1.2)	0.48	3.7	298
Tuber mass	Paterson		–	17.8 (1.4)	3.0 (1.8)	134 (20)	3.2 (2.9)	0.59	3.7	336
			+	17.1 (1.9)	0.0 (10.7)	56 (105)	1.1 (4.4)	0.47	3.7	178
		Roza	–	g plant <sup>–1</sup>	g plant <sup>–1</sup>	g ae ha <sup>–1</sup>			g plant <sup>–1</sup>	g ae ha <sup>–1</sup>
			+	0.90 (0.07)	0.00 (0.34)	86 (39)	1.4 (2.6)	0.57	0.05	> 560
	Roza	Early	–	0.89 (0.06)	0.00 (0.14)	89 (45)	2.0 (2.9)	0.62	0.05	367
			+	0.56 (0.06)	0.02 (0.06)	230 (163)	10.1 (35)	0.49	0.05	293
		Late	–	0.26 (0.03)	0.00 (0.06)	122 (37)	2.2 (2.5)	0.41	0.05	254
			+							

<sup>a</sup> Abbreviations: GDD, growing degree days; CPB, Colorado potato beetle; FRD, fixed response dose.

<sup>b</sup> Herbivory level in the absence (–) and presence (+) of CPB.

<sup>c</sup>  $D$  is upper asymptote;  $C$  is lower asymptote;  $I_{50}$  is fluroxypyr dose eliciting 50% response relative to dose = 0;  $b$  is slope at  $I_{50}$  dose;  $Y_{95}$  quantifies the plant response that results in a 95% reduction in the absence of herbivory; FRD quantifies the herbicide dose required to reduce the response variable to  $Y_{95}$ .

<sup>d</sup> FRD estimates followed by an asterisk differ significantly between herbivory levels based on nonoverlapping 95% confidence intervals.

TABLE 5. Season-long field bioassays (> 3,100 GDD after herbicide application): parameter estimates for the effects of fluroxypyr dose and CPB herbivory on potato tuber number and biomass (SE in parentheses).<sup>a</sup>

Response variable	Herbivory <sup>b</sup>	<i>D</i> <sup>c</sup>	<i>C</i>	<i>I</i> <sub>50</sub>	<i>b</i>	<i>R</i> <sup>2</sup>	<i>Y</i> <sub>95</sub>	FRD <sup>d</sup>
		no. plant <sup>-1</sup>	no. plant <sup>-1</sup>	g ae ha <sup>-1</sup>			no. plant <sup>-1</sup>	g ae ha <sup>-1</sup>
Tuber number	–	34.0 (2.2)	3.9 (5.8)	77 (52)	1.7 (2.7)	0.68	5.4	434*
	+	20.5 (2.1)	2.3 (3.9)	75 (125)	2.3 (3.9)	0.48	5.4	154*
		g plant <sup>-1</sup>	g plant <sup>-1</sup>	g ae ha <sup>-1</sup>			g plant <sup>-1</sup>	g ae ha <sup>-1</sup>
Tuber mass	–	8.0 (0.5)	0.1 (2.4)	40 (77)	1.1 (2.6)	0.81	0.5	> 560*
	+	5.1 (150)	0.0 (7.0)	1 (128)	0.5 (13)	0.71	0.5	85*

<sup>a</sup> Abbreviations: CPB, Colorado potato beetle; GDD, growing degree days; FRD, fixed response dose.

<sup>b</sup> Herbivory level in the absence (–) and presence (+) of CPB.

<sup>c</sup> *D* is upper asymptote; *C* is lower asymptote; *I*<sub>50</sub> is fluroxypyr dose eliciting 50% response relative to dose = 0; *b* is slope at *I*<sub>50</sub> dose; *Y*<sub>95</sub> quantifies the plant response that results in a 95% reduction in the absence of herbivory; FRD quantifies the herbicide dose required to reduce the response variable to *Y*<sub>95</sub>.

<sup>d</sup> FRD estimates followed by an asterisk differ significantly between herbivory levels based on nonoverlapping 95% confidence intervals.

## Field Bioassays: Season-long

Although short-season bioassays were aimed at characterizing volunteer potato fitness over a brief period, season-long bioassays were used to evaluate these treatments over a longer period. As a result, potatoes had more time to grow and were subjected to more CPB feeding. CPB population densities were similar to results of short-season bioassays until 8 and 12 WAT. In herbivory plots, total density at 8 WAT averaged 51.1 CPB plant<sup>-1</sup>, with predominantly adults being observed by 12 WAT (data not shown).

Tuber number and biomass response to fluroxypyr dose were affected by herbivory. Though tuber number was relatively unaffected by herbivory in short-season bioassays, repeated defoliation in season-long bioassays limited tuber production. The *D* parameter for tuber number was 40% lower with herbivory, compared with no herbivory (Table 5). In the absence of fluroxypyr, herbivory accounted for a loss of 3.1 g of tuber plant<sup>-1</sup>, although variability in the *D* parameter was considerably higher in the presence of herbivory, compared with no herbivory. This higher variability in potato response is believed to be largely the result of differential cumulative feeding, as the result of variation in naturally occurring CPB density within the herbivory-present treatment.

Less herbicide was needed to control the weed when herbivory occurred. Herbivory reduced the FRD 65 and > 85% for tuber number and tuber biomass, respectively (Table 5). Yield reductions from CPB herbivory exceed those of previous studies because fluroxypyr slowed plant growth and defoliation by CPB was more continuous as opposed to a single, simulated event (Cranshaw and Radcliffe 1980; Shields and Wyman 1984; Zehnder and Evanylo 1989).

## Management Implications

IWM systems targeting volunteer potato aim to reduce both tuber number and tuber biomass. Potato tuber density influences yield loss in onions (Williams et al. 2004) and carrots (M. Williams, unpublished data). Yield potential of potato increases with tuber biomass (Iritani et al. 1972; Wakankar 1944), and some herbicides are less effective on plants from large tubers, compared with those from smaller tubers (Lutman 1977b). In controlling volunteer potatoes, the effectiveness of shoot removal, using hand-hoeing or cultivation, improves when repeated or combined with the use

of herbicides (Boydston and Seymour 2002; Williams and Boydston 2002).

This study indicates that herbivory can significantly improve effectiveness of fluroxypyr applications for volunteer potato control. IWM systems are likely to be more effective when volunteer potato is defoliated, particularly when the weed is stressed by other tactics such as herbicide application. Feeding often reduced potato growth and reproduction, although contribution of CPB herbivory will be dependent on site-specific density, distribution, and growth of both arthropod and weed populations. Insecticide applications for arthropod pest control in the rotation crop could significantly decrease the potential role of herbivory from CPB by reducing CPB density and distribution.

Herbivory may be very important in determining the success of reduced herbicide doses. This is important to minor crop production where crop safety to herbicide use is often a concern. Small reductions in weed fitness caused by herbivory resulted in potentially large differences in the minimal dose required to control the weed. As an example, FRD reductions of 65 to > 85% in season-long bioassays with herbivory reflect the compounding stresses of delayed weed growth and herbivore load. Leaf consumption increases with larval development stage of CPB (Ferro et al. 1985), and sublethal doses of fluroxypyr were observed to slow or delay potato growth. Larvae feeding on treated plants during this time were, in effect, developing a greater capacity to defoliate, whereas the plant had limited ability to compensate. As more time passed before potato recovered from fluroxypyr application (i.e., as herbicide dose increased), loss of leaf area from herbivory compounded. Greater loss of leaf area would presumably reduce net photosynthesis thus intensifying effects the multiple stresses exerted on potato.

Although the model system examined in this study applies to cropping systems in rotation with potatoes, the concept of integrating arthropod herbivory and herbicide application may have broader application. As an example, solanaceous weeds infest annual cropping systems throughout the United States and Canada (Ogg and Rogers 1989; Ogg et al. 1981). CPB is a pest of potatoes and troublesome in some locations largely because of insecticide-resistant populations, which are difficult to control. Creating reservoirs of susceptible populations has been proposed as an approach to reducing selection pressure for insecticide resistance in CPB (Weber and Ferro 1994). However, several other ar-

thropod herbivores are associated with *Solanum* species (Olckers et al. 2002), and some are distributed throughout North America. Further study is needed to identify the extent to which herbivory may contribute to IWM outside of the context studied here and, in the case of CPB, implications this has on arthropod pest management of solanaceous crops.

## Sources of Materials

<sup>1</sup> Tops MZ, Gustafson LLC, 1400 Preston Road, Plano, TX 75093.

<sup>2</sup> Li-Cor model 3100, Li-Cor Corporation, 4421 Superior Street, Lincoln, NE 68504.

<sup>3</sup> Admire, Bayer Corporation, Crop Protection, Box 4913, Kansas City, MO 64120-0043.

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